

Simulating leaf area of corn plants at contrasting water status

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ARTICLE INFO

Article history:

Received 31 October 2008

Received in revised form 28 January 2009

Accepted 3 February 2009

Keywords:

Drought stress

Leaf area

Corn

Crop modeling

ABSTRACT

An exponential decay function was fitted with literature data to describe the decrease in corn leaf expansion rate as predawn leaf water potential decreases. The fitted function was then applied to modify an existing leaf area simulation module in a soil–plant–atmosphere continuum corn simulation model (MaizSim) in order to simulate leaf area of corn plants at different water status. Data were collected from field for two years as well as from sunlit growth chambers located at USDA-ARS facilities in Beltsville, MD with different irrigation frequencies. Comparison among simulations and measurements indicated that the modified leaf area module improved leaf area simulation for corn plant under different drought stress. For plants under more severe drought stress, the improvement in leaf area simulation was more significant. These results suggested that the modified leaf area model presented an approach to mechanistically link corn leaf area with corn plant water status, and was suitable for integration with existing corn models that simulate corn leaf area.

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1. Introduction

Green leaf area plays a critical role in different aspect of crop growth and development. Leaf area determines the fraction of incident photosynthetically active radiation (PAR) intercepted by crop canopy and ultimately dry matter production. Leaves also are the main path for transpiration and carbon harvesting. Therefore simulation of green leaf area during growing season has been a crucial component of crop growth model.

Green leaf area has been simulated with different approaches, such as discontinuous functions (Dale et al., 1980), or regression analysis (Baker et al., 1975). In some models (e.g. CERES, GOSSYM), leaf area is calculated from the biomass partitioned to the leaves, using the concept of specific leaf area. Some believe that it is appropriate to model leaf expansion independently of the plant carbon budget (Tardieu et al., 1999). In the models proposed by Arkebauer et al. (1995) and Fournier and Andrieu (1998), leaf expansion and leaf senescence are driven only by thermal time, and are simulated separately on a per leaf basis. This methodology has been adopted in some recently developed models (Lafargea and Tardieu, 2002; Guillermo et al., 2003; Lizaso et al., 2003; Yang et al., 2004; Fleisher and Timlin, 2006) for different crops such as

sun flower, potato and maize. These new models provide more flexible and robust ways in leaf area simulation. However, most of these models did not include provisions to mechanistically account for the effect of drought stress on leaf area.

It is known that a small reduction in the water potential of the root medium immediately decrease leaf growth of maize (Boyer, 1970; Acevedo et al., 1971, 1979). Under water-deficient conditions, cell elongation of higher plants can be inhibited by interruption of water flow from the xylem to the surrounding elongating cells (Nonami, 1998). Westgate and Boyer (1985) and Tanguilig et al. (1987) reported that leaf growth of maize was stopped when predawn leaf water potential was lower than -10.0 bar. Other studies (Sarah and Tardieu, 1997; Stone et al., 1998; Cakir, 2004) also showed that leaf areas of drought-stressed corn plants were smaller than those of well-watered plants.

The physiological processes that affect leaf growth under drought stress, such as cell wall mechanical properties (Cosgrove, 2005; Muller et al., 2007) or hydraulic properties of growing cells (Tang and Boyer, 2002; Bouchabké et al., 2006) have been extensively studied. Granier and Tardieu (1999) analyzed the effect of short-term water deficit on sun flower leaf development and found that even though water deficit did not affect the duration of expansion and division, it did reduce relative expansion rate by 36% and relative cell division by 39%.

Lecoeur et al. (1996) and Tardieu et al. (2000) developed mechanistic models in which final leaf area was calculated as the

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product of number of cells and size of cells. The models were capable of predicting the temporal development and final area of individual leaves in response to soil water deficits. However, since the interactions among the cellular processes and their linkages to responses at whole-plant level is insufficiently understood (Tardieu, 2003), modeling each cellular response would result in a large number of redundant mechanisms and an over-parameterization. The model recently introduced by Chenu et al. (2008) incorporated an existing model of leaf expansion in response to short-term environmental variations with a model coordinating the development of all leaves of a plant. The model did possess the capability of simulating leaf area of corn plant under drought stress. However, in their model, leaf expansion reduced linearly with reduction in leaf water potential. Yet data from other studies (Boyer, 1970; Tanguilig et al., 1987) reported a non-linear relationship between reduction in corn leaf expansion rate and predawn leaf water potential.

The goal of this paper was to modify an existing leaf expansion module which was originally developed by Lizaso et al. (2003), in a soil–plant–atmosphere continuum (MaizeSim-2DSOIL, Yang et al., 2008) model to simulate leaf area of corn plant at different water status, and to evaluate the performance of the modified leaf expansion module with data collected from growth chambers and fields.

2. Materials and methods

2.1. The model

A soil–plant–atmosphere model (MaizeSim-2DSOIL) was constructed by coupling a process-based corn simulation model (MaizeSim) and a two-dimensional finite element-based soil model (2DSOIL). MaizeSim has been developed by the Crop System & Global Change Laboratory (CSGCL) at USDA/ARS, Beltsville to simulate corn growth and development as a function of key environmental variables. In the coupled model, MaizeSim is responsible for simulating corn growth and development as a function of light, temperature, humidity, CO₂, etc. The model adopts the biochemical C4 photosynthesis model (Von Caemmerer, 2000) and the BWB paradigm of stomatal conductance (Ball et al., 1987) to simulate stomatal conductance, photosynthesis and transpiration of a corn plant. Leaf expansion is simulated with the model proposed by Lizaso et al. (2003). The 2DSOIL model is a modular, comprehensive two-dimensional soil simulator that is specifically designed to be combined with existing plant models (Timlin et al., 1996). Modules of 2DSOIL simulates water, solute, heat and gas movement, as well as root activity of plants in a two-dimensional soil profile which is partitioned into multiple layers. Coupling MaizeSim with 2DSOIL provides a soil–plant–atmosphere continuum system which possesses the potential of taking into account the information of dynamic soil water status in simulating corn growth and development (Yang et al., 2008).

Functions introduced by Lizaso et al. (2003) and Fournier and Andrieu (1998) were originally adopted and modified in MaizeSim to simulate corn leaf expansion. To facilitate the discussion, a brief description of the functions is also presented in this manuscript.

To simulate leaf expansion of corn plant at different water status, a plant water status effect function $f(\varphi_{\text{dawn}})$ was introduced in the equation proposed by Lizaso et al. (2003)

$$\text{GRE}_i = f(\varphi_{\text{dawn}})(Ae_i k_{e_i}) \frac{e^{-k_{e_i}(t-t_{e_i})}}{(1 + e^{-k_{e_i}(t-t_{e_i})})^2} \quad (1)$$

In the equation, Ae_i is the final surface area of the i th leaf (cm²), t_{e_i} is the thermal time when the leaf reaches 50% of its final area

(growing degree days after emergence), and k_{e_i} is a unitless parameter controlling the slope of the curve.

Ae_i is described using a modification of the relationship proposed by Dwyer et al. (1992) (Lizaso et al., 2003)

$$Ae_i = Ae_x e^{A_1((LN_i - LN_x)/(LN_x - 1))^2 + A_2((LN_i - LN_x)/(LN_x - 1))} \quad (2)$$

where Ae_x and LN_x are the area (cm²) and nodal position of the largest leaf blade, respectively. Calculation of Ae_x followed what was proposed by Muchow and Carberry (1989) and Dwyer et al. (1992), where Ae_x was a function of both the total number of leaf and leaf length characteristic of the genotype.

LN_i is the nodal position of the i th leaf. A_1 and A_2 are two parameters that can be estimated from the total number of leaves LT (Fournier and Andrieu, 1998), which is an input to the model, and is defined by the characteristic of the genotype:

$$A_1 = -10.61 + 0.25LT \quad (3)$$

$$A_2 = -5.99 + 0.27LT \quad (4)$$

Nodal position of the largest leaf, LN_x , is expressed as a linear function of the total number of leaves (Birch et al., 1998)

$$LN_x = 0.67LT \quad (5)$$

The thermal time needed to expand the i th leaf to 50% of its final area is calculated with the following equation:

$$t_{e_i} = tt_i + \frac{2.197}{k_{e_i}} \quad (6)$$

According to Lizaso et al. (2003), first and second leaves had a t_{e_i} parameter of 25 and 50 GGD8, respectively. For other leaves, the value of tt_i is calculated as

$$tt_i = (LN_i - 2)PHY + tt_2 \quad (7)$$

where LN_i is the nodal position of the i th leaf, PHY the phyllochron (GGD8), and tt_2 the thermal time from emergence to the appearance of the second leaf.

$$k_{e_i} = k_0 + k_x e^{-(LN_i - 1)^2 / 2W_k^2} \quad (8)$$

where $k_0 = 0.02$ and $k_x = 0.2$ (Lizaso et al., 2003).

W_k is a linear function of the total number of leaves

$$W_k = \frac{LT}{8.18} \quad (9)$$

In Lizaso et al. (2003), potential leaf expansion rate is driven only by temperature, therefore $f(\varphi_{\text{dawn}}) = 1$ (original method). However, it is known that plant water status also affects leaf expansion rate. In this study, in an effort to simulate the effect of plant water status on leaf expansion rate (modified method), $f(\varphi_{\text{dawn}})$ was expressed in the following exponential decay equation

$$f(\varphi_{\text{dawn}}) = \frac{1 + e^{a \times b}}{1 + e^{b \times (a - \varphi_{\text{dawn}})}} \quad (10)$$

Eq. (10) describes the decrease in leaf expansion rate in reaction to reduction in predawn leaf water potential. In the equation, φ_{dawn} is predawn leaf water potential, a is the reference predawn leaf water potential at which point leaf expansion rate decreases to 50% of its potential. And b is the sensitivity parameter that controls the shape of the decaying curve.

The data set used to develop the exponential decay function (function (10)) was collected from literatures. Boyer (1970) reported that leaf elongation of corn plants was inhibited at low leaf water potential. In the study reported by Tanguilig et al. (1987), predawn leaf water potential started from -0.5 bar. When predawn leaf water potential dropped to -1.1 bar, leaf expansion was significantly reduced. This seems to agree with what was

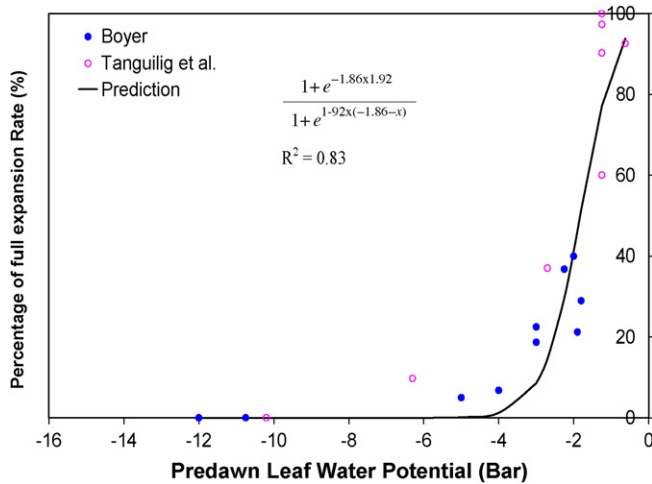


Fig. 1. The function that describes the reaction of leaf expansion to predawn leaf water potential. Data points were pooled from Boyer (1970) and Tanguilig et al. (1987).

reported by Boyer (1970). To make sure the plant water status effect function covers a more complete range of predawn leaf water potential, data from both Boyer (1970) and Tanguilig et al. (1987) were pooled together (Fig. 1).

SAS (The SAS system for Windows, 9.01, SAS Institute, Inc., Cary, NC, USA) PROC NLIN was applied to fit the plant water status effect function (Eq. (10)) with the pooled data set. Eq. (10) fitted with data collected from Boyer (1970) and Tanguilig et al. (1987) quite well. The R^2 value of the fitted function was 0.83 (Fig. 1).

Predawn leaf water potential in Boyer (1970) was mostly lower than -2 bar, at which point the leaf expansion rate was already reduced to lower than 40% of the potential rate. Tanguilig et al.'s (1987) data, on the other hand, covered a wider range in leaf water potential, reducing from 0 bar to -10.25 bar. The general trend of both data sets, however, agreed with each other. In the two data sets, the magnitude of reduction in leaf expansion rate in relation to predawn leaf water potential also agreed with each other quite well (Fig. 1). The PROC NLIN procedure returned values of -1.86 and 1.92 , respectively, for coefficients a and b in Eq. (10). The reference leaf water potential at -1.82 bar means that when leaf water potential decreased to this value, the leaf expansion rate will be 50% of the potential leaf expansion rate. This agreed with what was reported by Acevedo et al. (1971).

2.2. The data

Data from both growth chambers and fields were used to evaluate the performance of the modified leaf simulation module in the MaizSim-2DSOIL soil–plant–atmosphere model. The chamber data used for analysis in this paper were acquired from an experiment in which corn response to CO_2 enrichment and drought was studied. The experiment was conducted in naturally sunlit, controlled environment Soil–Plant–Atmosphere–Research (SPAR) chambers at the Beltsville Agricultural Research Center, Beltsville, Maryland, USA (Kim et al., 2006). The physical configuration of these chambers and methods of environmental control have been described by Baker et al. (2004). Maize plants (*Zea mays* L. cv. Pioneer hybrid 3733) were grown on a mixture of sterilized sand and vermiculite (1:1 by volume). Maize seed was sown on 28/May/2004. Plant density in each chamber was maintained at 12 plant m^{-2} . Leaf area of each plant was monitored by measuring the length and width of each leaf with a ruler.

Data from three SPAR chambers with different irrigation levels were chosen for analysis. In all three chambers, PAR levels inside

and outside the chambers were measured with quantum sensors (LI-190SB, LI-COR, Inc., Lincoln, Nebraska, USA). The atmospheric CO_2 level was controlled at $370 \mu\text{mol mol}^{-1}$ during daytime. During the experiment, air temperature inside the chambers was set to $27/27^\circ\text{C}$ (day/night) early in the experiment and $27/16^\circ\text{C}$ later in the experiment. Relative humidity inside the chambers was monitored but not controlled. Irrigation was varied in each of the chamber. The fully irrigated treatment was irrigated to fully replace water lost by evapotranspiration (ET). The “50%” treatment was fully irrigated until 39 days after emergence (DAE) and then irrigation was withheld. Irrigation in the “25%” treatment chamber was withheld for most of the time from the beginning of the experiment, and when the plants were re-irrigated, the irrigation rate was lower than that in the control chamber (Fig. 2). For each chamber, soil volumetric water content was recorded by fifteen time domain reflectometry (TDR) waveguides installed at five depths, replicated at three horizontal positions (Timlin et al., 2007).

Field data were collected from the Wye Research and Education Center fields (38.91°N , 76.15°W) in year 2006 and 2007. Plants in the field were not irrigated, so the only source of water to the plants came from rain fall. In both years, maize hybrid PI 34M91 were planted. In year 2006, seeds were sown on May/12/2006. In 2007, planting was done on May/14/2007. In both years, plant density in the field was 6.4 plants m^{-2} with a row spacing of 76 cm. Plants were sampled every two weeks starting from V2 to V3 stage.

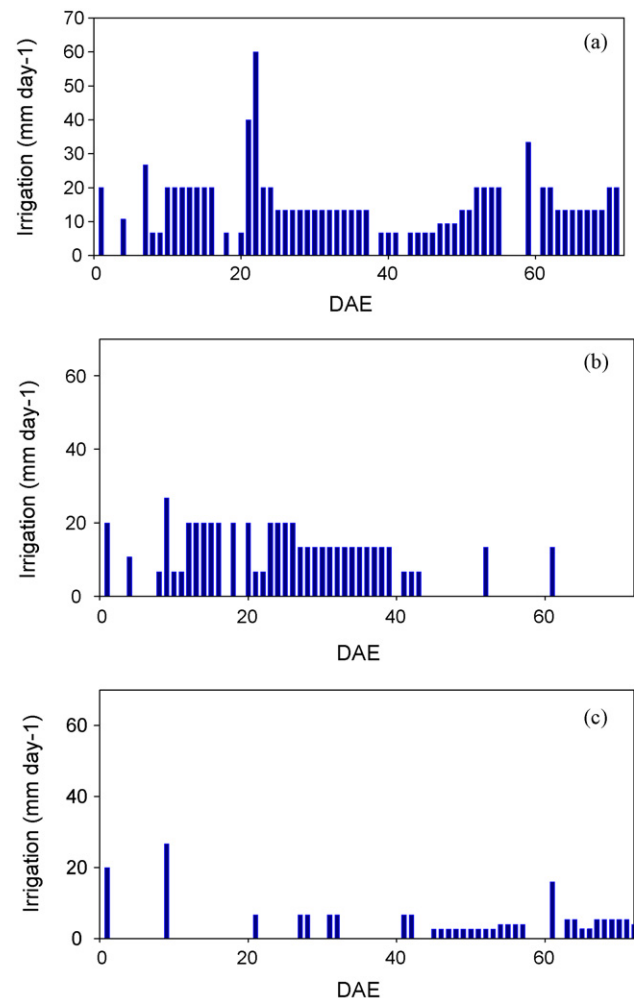


Fig. 2. Daily irrigation rate in the well-irrigated (a), “50%” treatment (b) and “25%” treatment (c) from a three growth chamber experiment with corn.

Table 1

Performance evaluation results for leaf area simulation of corn plants treated with different irrigation frequencies in the SPAR chambers.

	RMSE		ME		EF		D	
	Without drought stress effect function	With drought stress effect function	Without drought stress effect function	With drought stress effect function	Without drought stress effect function	With drought stress effect function	Without drought stress effect function	With drought stress effect function
Well watered	954.3	839.5	635.8	464	0.796	0.842	0.95	0.959
50% Treatment	968.7	810.7	773.7	590	0.764	0.835	0.944	0.958
25% Treatment	1705.5	590.5	1496.5	398.4	-0.506	0.782	0.787	0.947

At each sampling, thirty plants were harvested to measure number of leaves, leaf area, weight of leaves, etc. of each plant. An automatic weather station was set up to collect data on radiation, rain fall, temperature, relative humidity, etc. during the growth seasons.

2.3. Performance evaluation

To evaluate the deviation of the leaf area simulation, statistics of mean error or bias (*ME*), root mean square error (*RMSE*), model efficiency (*EF*), as well as Willmott's index of agreement (*D*) were calculated by Eqs. (11)–(14). *EF* is a measure of deviation between model output and the measured values relative to the scattering of the measured data. The value of *EF* will be 1 if simulated values matches the measured values perfectly. *D* varies from 0.0 (poor model) to 1.0 (perfect model) (Willmott, 1981; Willmott et al., 1985).

$$ME = \frac{\sum_{i=1}^N (y_i - Y_i)}{N} \quad (11)$$

$$RMSE = \sqrt{\frac{\sum_{i=1}^N (y_i - Y_i)^2}{N}} \quad (12)$$

$$EF = 1 - \frac{\sum_{i=1}^N (y_i - Y_i)^2}{\sum_{i=1}^N (y_i - \bar{y})^2} \quad (13)$$

$$D = 1 - \frac{\sum_{i=1}^N (y_i - Y_i)^2}{\sum_{i=1}^N (|Y_i - \bar{y}| + |Y_i - \bar{y}|)^2} \quad (14)$$

3. Results

Comparison among simulated leaf area with leaf area measured in SPAR chambers showed that different irrigation treatment resulted in different leaf area, and that leaf area simulated with the modified leaf area function agreed with measurements better than those simulated with the original leaf area function (Table 1, Fig. 3). Further comparisons also showed that the improvement was more significant as the water stress became more severe.

For plants in the fully irrigated chamber, leaf area per plant increased steadily to around 5300 cm² about 45 days after emergence (Fig. 3a). Leaf areas simulated with the original leaf expansion function followed the trend pretty well. The *D* value of leaf area simulated this way was 0.975. Yet Fig. 3a showed that leaf areas simulated with the original method overestimated leaf area through the season. The *D* value of the leaf areas simulated with modified method increased to 0.981. Even though it seemed to be a small improvement, from Fig. 3a it can be seen that the simulation was obviously closer to measurements than those simulated with the original method. Values of *RMSE* and *ME* of leaf areas simulated with the predawn leaf water potential effect function was reduced by 15.2% and 36% respectively. The size of *RMSE* as the percentage

of the mean leaf area decreased from 23% to 19%. The value of *EF* also increased slightly.

For plants in the 50% treatment, simulation of leaf area was also improved with the predawn leaf area effect function. Leaf area per plant in this treatment increased to over 5000 cm² after 45 DAE, which was similar to those in the well-watered chamber. But at the

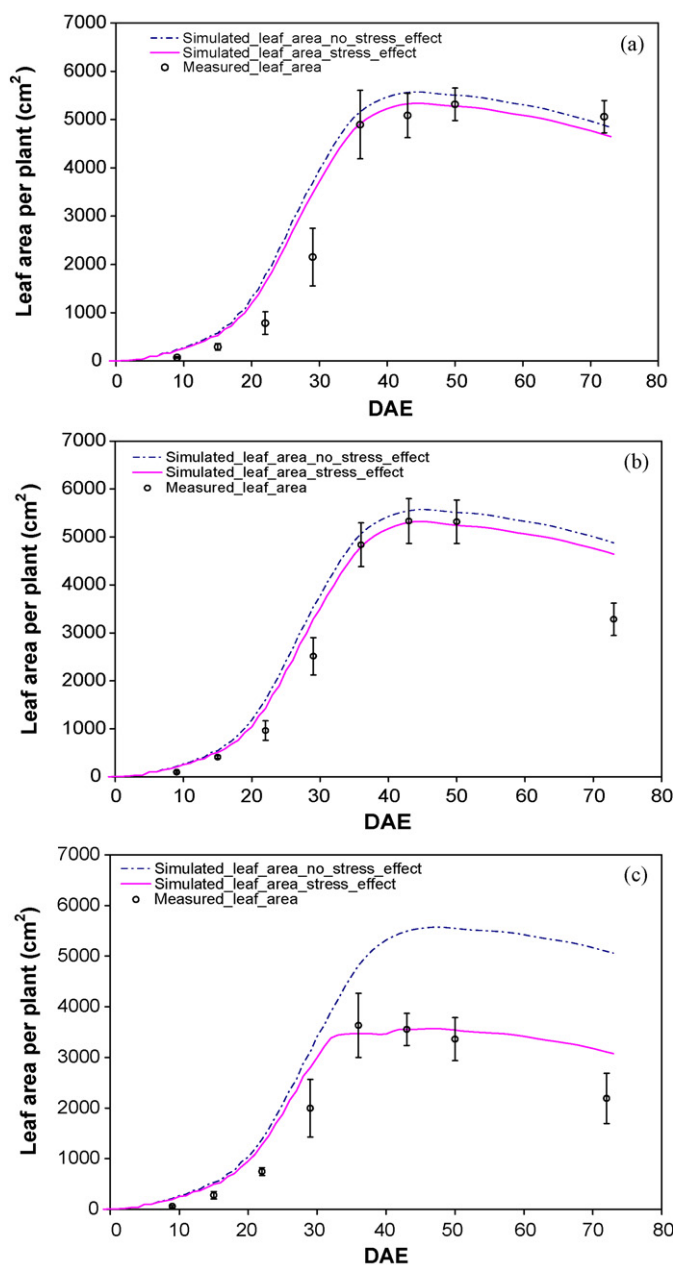


Fig. 3. Measured and simulated leaf area in the well-irrigated (a), "50%" treatment (b) and "25%" treatment (c).

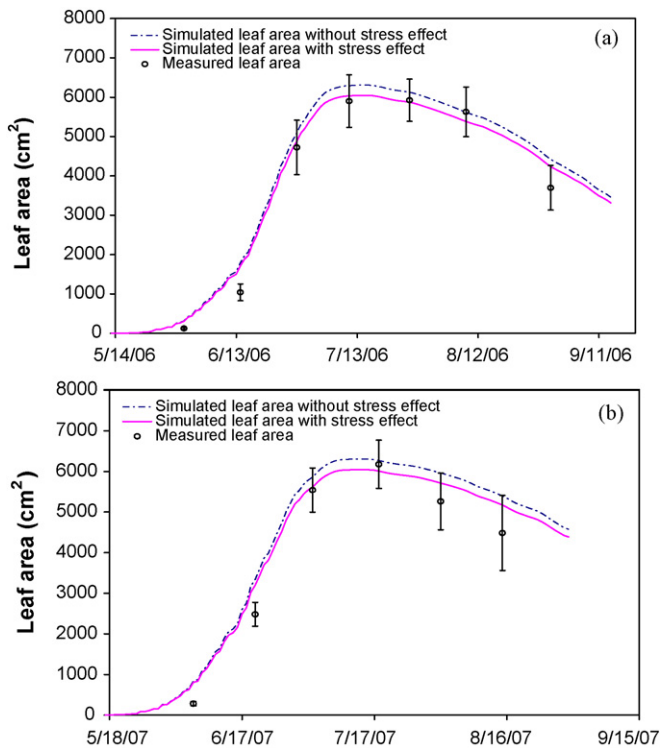


Fig. 4. Measured and simulated leaf area in the well-irrigated (a), “50%” treatment (b) and “25%” treatment (c).

end of the experiment, the leaf areas in this chamber were much smaller. Leaf areas simulated with both the original and modified methods followed the general trend quite well. However, leaf areas simulated with the original method overestimated the measurements, while the ones simulated with the modified method reduced the overestimation and were closer to measurements (Fig. 3b). *RMSE* and *ME* were reduced by 18% and 32%, respectively (Table 1), for the leaf areas simulated with the modified method. Values of *EF* and *D* of the leaf areas simulated with the modified method were increased. However, both the original method and the modified method overestimated leaf area late in the season.

Agreement between simulated and measured leaf areas of the plants in the 25% treatment was significantly improved with the modified method. Leaf areas of the plants in this treatment only increased to around 3500 cm². The original method was not able to simulate this dramatic decrease in leaf area caused by drought stress, and overestimated leaf area by more than 2000 cm² (Fig. 3c). Values of *EF* and *D* of leaf areas simulated with the original method were −0.278 and 0.817, respectively, indicating that the original model was not able to follow the general trend in leaf area expansion for plants under severe drought stress. On the other hand, Fig. 3c showed that leaf areas simulated with the modified method was able to follow the trend of leaf area in this treatment. Values of *EF* and *D* were improved to 0.852 and 0.958, respectively, and values of *RMSE* and *ME* were reduced by 69% and 74%, respectively, with the modified method (Table 1).

Simulated leaf area with the modified methods agreed with the field measurements better in both year 2006 and year 2007 (Fig. 4, Table 2). In year 2006, the total rain fall during the season was 750 mm cm⁻² (Fig. 4). Leaf area per plant in the field increased to 5900 cm² (Fig. 4a). Values of *EF* and *D* indicated that both the original and modified methods were able to follow the general trend in leaf area. However, leaf areas simulated with the modified method were closer to measurements. Values of *RMSE* and *ME* were reduced by 12% and 46%, respectively, when leaf area was simulated with the modified method. The size of *RMSE* as the percentage of the mean leaf area was reduced from 16% to 13%. In year 2007, total rain fall during the season was 300 mm cm⁻². Leaf area per plant increased to 6100 cm² (Fig. 4b). Values of *EF* and *D* were comparable to simulations of 2006, albeit a little lower. When simulating with the modified method, *RMSE* and *ME* values were reduced by 20% and 33%, respectively. And the size of *RMSE* as the percentage of the mean leaf area was reduced from 17% to 13%.

4. Discussion

When simulating leaf area of well-watered plants, it is usually assumed that leaf area expansion is only driven by thermal time and that leaf water potential does not decrease enough to affect leaf expansion. However, simulation using the data from the well-watered chamber in 2004 showed that on 7/29/04, the predawn leaf water potential of the well-watered plants decreased to −0.1 bar. According to Eq. (2), at −0.1 bar, the leaves will expand at 99.4% of the potential rate. Through the season, the accumulation of this kind of minor decrease in leaf expansion rate from the potential rate would prevent a leaf from reaching its potential final area. The original leaf area model by Lizaso et al. (2003) only considered thermal time as the driving force for leaf area expansion, therefore this kind of minor reduction in leaf area expansion was not included in the original simulation. After adding the predawn leaf water potential function developed in this study into leaf area simulation, the minor decrease in leaf area expansion caused by minor decrease in predawn leaf water potential was then included in the simulation. This might explain why the modified method we developed in this study simulated better than the original model (Lizaso et al., 2003) even for simulation of leaf area of well-watered plants.

For the 50% treatment in the growth chamber, water was not withheld until DAE 39. Up to that day, soil water content was kept at similar level to those of the fully irrigated treatment. Therefore both the measured and simulated leaf areas were similar to those of the fully irrigated treatment. After the irrigation was withheld, soil water content decreased more than 40% from DAE 47 to DAE 51. The simulated leaf water potential decreased because of the decrease in soil moisture level during the same period. Lower leaf water potential would reduce leaf expansion rate, resulting in smaller leaves. This might explain why leaf areas simulated with the modified method was closer to measurements than those simulated with the original method.

As indicated by Tardieu et al. (2000), when water deficit occurred later in leaf development, it reduced final leaf area to a lesser extent than early deficits of similar intensity. Therefore, the

Table 2

Performance evaluation results for leaf area simulation of plants collected from field in year 2006 and 2007.

	<i>RMSE</i>		<i>ME</i>		<i>EF</i>		<i>D</i>	
	Without drought stress effect function	With drought stress effect function	Without drought stress effect function	With drought stress effect function	Without drought stress effect function	With drought stress effect function	Without drought stress effect function	With drought stress effect function
2006 Field data	607.4	536.3	374	198.5	0.92	0.94	0.979	0.984
2007 Field data	672.4	542.5	571.7	380.5	0.89	0.91	0.971	0.981

leaf area in the 50% treatment was only slightly smaller than the leaf area of plants in the fully irrigated chamber. Water stress in corn could cause early leaf senescence (Granier and Tardieu, 1999). However the simulated senescence rate in the model was not linked to plant water status. This may have been one of the main reasons the model overestimated leaf area late in the season for the 50% treatments.

Irrigation to the plants in the 25% treatment of the experiment conducted in chambers was withheld early in the season (Fig. 2), resulting in low soil moisture early in the season. Early in the season, plant leaf area would go through an exponential increase stage (Yang et al., 2004). The lowered soil moisture, and therefore predawn leaf water potential, drastically decreased the expansion rate during this exponential increase stage. This is why the modified method developed in this study, with Eq. (10), was able to follow the trend in leaf area of the drought-stressed plants, while the original method (Lizaso et al., 2003) seriously overestimated the measurements.

Data from Boyer (1970) and Tanguilig et al. (1987) were collected from the youngest leaf on a plant. In the Boyer (1970) study, observations were done from leaf six, which was the youngest leaf measured during the experiment. In Tanguilig et al. (1987), data were collected from youngest fully expanded leaves at each measurement. The reduction in leaf expansion rate in reaction to leaf water potential may be different for leaves of different ages. However, in this study the reaction to reduced leaf water potential was assumed to be the same for all leaves. This might have caused the overestimation of leaf area early in the season. The limited carbon capacity of young seedlings and other biotic pressures such as stand uniformity, soil fertility may also restrict leaf expansion. Yet, in this study, leaf expansion is only a function of temperature and leaf water status. These factors that are not considered in the model may have also contributed to the model overestimation of leaf area early in the season.

Begg and Turner (1970) and Chone et al. (2001) also indicated that the leaf water potential of leaves at different height was different. In the simulations of this study, leaf water potential was assumed to be the same for all leaves. All these may have contributed to the difference between simulation and measurement for plants under water stress. Therefore, even though the leaf area simulation with the modified method was much improved over simulation with the original method, the simulation of leaf area under drought stress was not as good as the simulation of leaf area of well-watered plants. Since there were ample amount of rain fall in year 2006, yet not a lot in 2007, it could be assumed that plants in year 2007 in the field were under more drought stress than those in year 2006. Therefore, the simulation did not fit the measurement in 2007 as well as in 2006.

In the models introduced by Lizaso et al. (2003) and others (Lafargea and Tardieu, 2002; Guillermo et al., 2003), leaf expansion rate is constant per unit thermal time under optimal environmental conditions (Sadok et al., 2007). Also, the maximum leaf expansion rate is unique for all leaves of a plant, and depends on the rank of each leaf (Andrieu et al., 2006). By introducing the function that describes the reduction in leaf area expansion rate in relation to decrease in predawn leaf water potential, we did not alter these fundamental frame works. However from the presented data, it can be seen that by adding a function that mathematically links plant water status with leaf expansion rate, the leaf area simulation could be closer to measurement, especially when the plants were under drought stress. Even though more studies should be conducted to set up the relationship between senescent rate and drought stress, and to study the reduction in expansion rate of leaves of different ages, constructing mathematical function that mechanistically describes the reaction of leaf expansion rate to decrease in leaf water potential

is a method worth probing in simulating plant growth under drought stress.

5. Conclusion

Data were collected from literatures to fit with a function that described the reduction in leaf expansion rate in reaction to decrease in predawn leaf water potential. The fitted function was applied to modify an existing corn leaf area simulation module, which was then incorporated in a soil–plant–atmosphere corn simulation model. Performance evaluation with both chamber and field data showed that when leaf area was linked to leaf water status using the developed predawn leaf water potential effect function in leaf area simulation, the simulated leaf areas were closer to measurements from plants at different water status. It was also noticed that the improvement in leaf area simulation was more obvious for plants under more severe drought stress.

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